

HOST SPECIFICITY IN RAIDING BEHAVIOR
OF THE SLAVE-MAKING ANT
POLYERGUS LUCIDUS

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In the pine barrens of Suffolk County, New York, at least three species of *Formica* (subgenus *Neoformica*) are used as slaves by the obligatory slave-making ant *Polyergus lucidus*. In any single nest, however, only one slave species may be found. This contrasts with the sympatric, facultative slave-making ants of the genus *Formica* (subgenus *Raptiformica*) in which single colonies often contain two or more species of slaves. The slave species exclusivity of *P. lucidus* might result in two ways: (1) raids could be made to only one slave species of the four available; or (2) raids could be made to more than one slave species, but the captured pupae could be consumed differentially by the resident slaves, favoring the survival to eclosion of only one slave species. This paper reports the results of a study demonstrating that colonies of *P. lucidus* will, if given a choice, raid only colonies of the slave species already present in the mixed nest. Since scouts typically lead nestmates to target *Formica* nests (Cool-Kwait & Topoff, 1984), this selective process must occur through the perceptions and actions of the scouts.

METHOD

The field study was conducted on a two-acre site in Suffolk County previously described in Goodloe & Sanwald (1985). Two colonies of *P. lucidus* were collected in late spring of 1985 near Rocky Point, N.Y. One colony, P/S#1, contained slaves of the species *Formica schaufussi*, and the other, P/N#10 contained *Formica nitidiventris* slaves. Each colony was placed in a portable artificial

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nest contained within a $61 \times 43 \times 10$ cm plywood box. The nest consisted of a plastic box filled with moistened dirt inserted into a larger plywood box and having a single entrance/exit hole. A similar entrance/exit hole from the plywood box to the outside was closed with a plastic plug which could be removed to allow raiding to occur. The lid of the plywood box was removable to allow examination of the nest and the activity of *P. lucidus* workers prior to raiding. A cardboard cover was placed over the plastic nest box to prevent disturbing the colony when the lid was lifted, and was removed only when the interior of the nest was examined.

Experience has shown that very large colonies of *P. lucidus* are able to make multiple raids in a single day (Sanwald, unpublished observations). To maximize the frequency of raids for this study, each colony was expanded, prior to the beginning of the experiment, by the addition of slave-makers and slaves of the appropriate species. The colonies were expanded until each included approximately 1300 raiders and 4000 slaves at the beginning of the raiding season. Normal colonies usually contain several hundred slave-makers and slaves. This mixing procedure was possible because *P. lucidus* workers and slaves from different colonies can be successfully mixed when they are from colonies containing the same slave species (Goodloe & Sanwald, unpublished data). Such mixes between any combination of adult slaves and slave-makers from colonies using different slave species have been impossible to achieve.

Initially, each colony contained a single *P. lucidus* queen. The artificial colonies were kept indoors and observed until larvae appeared in the nest, from which time the colonies were allowed opportunities to raid.

A fixed location was chosen on the two-acre site from which raids were allowed to occur. On every day when weather was favorable for raiding, between 1300 and 1400 hr, one of the colonies was brought outside and placed at this location. The plug was removed to allow passage in and out of the artificial nest. To prevent slaves from initiating an emigration out of the artificial nest, all emerging slaves were retrieved by hand and returned to the artificial nest at the end of the day. All *P. lucidus* workers, by contrast, were allowed to pass in and out so that raids could occur.

Observations were made until the raiders had returned from any raids that occurred and activity of the slave-makers in and out of the

nest ceased. The artificial nest was then replugged and returned inside until the next raiding opportunity. The two colonies were allowed to raid on alternate days at the fixed location within the constraints of differences in time of onset of raiding activity.

Samples of slave species workers were taken from each raided colony, when possible, for identification (see Appendix). Data were analyzed using the binomial test for large samples to determine if the choice of species raided was non-random. Expected P for random choice was set at .5 because both slave species were equally available to the raiders.

RESULTS AND DISCUSSION

The results of this study are summarized in Table 1. Between June 1 and August 3, 1985, Colony P/S#1, containing *F. schaufussi* slaves, made 45 raids. Samples of raided workers were obtained for 44 of these raids. In the blind identification of samples, 43 were determined to be *F. schaufussi* and one was *F. nitidiventris*. Choice of host species to raid was non-random ($p < .00003$, $n = 44$).

Colony P/N#10, containing *F. nitidiventris* slaves, conducted a total of 32 raids. Worker specimens were obtained for 28 of the raided colonies. Of these, 25 were identified as *F. nitidiventris*, one as *F. schaufussi*, and two as indeterminate, possible *F. incerta*. Again choice of host species was non-random ($p < .00003$, $n = 28$). The raid of P/S#1 on the *F. nitidiventris* netted approximately 50 pupae, while the raid of P/N#10 on the *F. schaufussi* nest netted 5 pupae. These numbers are low, but there is no evidence to determine whether the raiders were less interested in the pupae of these species or if the raided nests were already depleted of pupae.

Table 1. Slave species raided by *P. lucidus* colonies.

	Same	Different	Inter- mediate***	Total
P/S#1*	43	1	0	44
P/N#10**	25	1	2	28

**P. lucidus* colony with *F. schaufussi* slaves

***P. lucidus* colony with *F. nitidiventris* slaves

***intermediate in characters between the two slave species

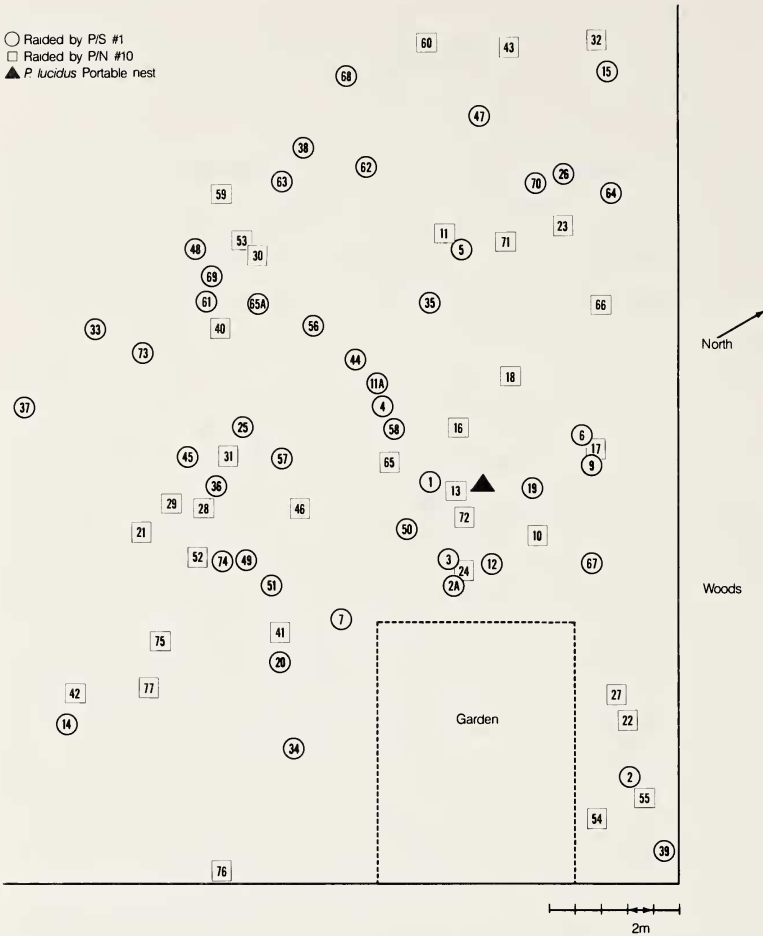


Fig. 1 Spatial distribution of raids by *Polyergus lucidus*. Numbers represent temporal order of raids during the 1985 season.

A more impressive demonstration of the species exclusivity of raiding in these colonies can be seen in Figure 1, where a spatial distribution of the raids is shown. The raided nests constitute a majority (estimated to be at least 75%) of the total available slave species nests in the described area.

There was no overlap between the two raiding colonies: none of the slave species nests were raided by more than one *P. lucidus* colony although several colonies were subjected to multiple raids by

the same colony. P/S#1 raided slave colony #1 four times, colony #11A three times, and colonies #5, #9, #11, #34, #50, and #61 twice. P/N#10 raided slave colony #41 three times, and colonies #19, #21, and #58 twice.

It is clear from this study that raids are conducted almost exclusively to colonies of the same slave species found in the raiders' home nest. However, this experiment addressed the question of whether preference would be shown given abundant and equal availability of both species. Yet to be explored is the question of whether the raiders would choose alternative targets if the preferred slave species was absent.

Additional evidence has indicated that pupae of a slave species other than the species present in a given *P. lucidus* nest are more likely to be consumed (Goodloe and Topoff, unpublished data). Thus it seems unlikely that workers of any slave species other than the original host species will survive in the nest.

Goodloe and Sanwald (1985) demonstrated that newly mated *P. lucidus* queens, given a choice between a colony of the slave present in their nest of origin and a colony of another equally available slave species, will choose to invade the former. Although the mechanism by which raiders and queens acquire their preferences is unknown, imprinting is a likely possibility. For several *Formica* species, newly eclosed workers imprint to the species of pupae present during their first 15 days (Jaisson, 1975; Le Moli & Passetti, 1977; Le Moli & Mori, 1982). Perhaps *P. lucidus* queens and workers imprint to the slave species present at the time of their eclosion. The next step will be to determine if *P. lucidus* female alates are influenced, in their mate choice, by the host species in the male's colony of origin.

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APPENDIX

Identification of Slave Species

Currently existing published keys proved insufficient to distinguish *Neoformica* species. Specimens obtained from raided nests

were identified, without knowledge of the slave species of the raiders, according to the following criteria:

1) *Formica schaufussi*: Specimens reddish to yellowish brown on the head and alitrunk (=thorax). Gaster usually darker. Head and alitrunk usually concolorous, head sometimes slightly darker, never as dark as gaster. Body size typically large.

2) *Formica nitidiventris*: Specimens distinctly brown. In mature workers head and gaster shiny medium brown, alitrunk sometimes concolorous, sometimes lighter with brown infuscation on dorsal surface. Younger workers usually have a lighter alitrunk: yellowish brown with brown infuscation on the dorsal surface. Body size usually small to medium.

3) Specimens fitting into neither of the above categories. These ants have the dark heads and gasters characteristic of *Formica incerta* but there are too few workers in the samples to provide confidence in this label. The alitrunk color is yellowish or reddish yellow but dark infuscation appears on some specimens.

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